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AGONISTIC BEHAVIOR IN SHORT-BILLED DOWITCHERS FEEDING ON A PATCHY RESOURCE

Elizabeth P. Mallory and David C. Schneider

Aggressive behavior in migratory shorebirds occurs primarily between foraging individuals and probably depends on such factors as density of foraging shorebirds, foraging methods, and density and patchiness of prey items (Recher and Recher 1969, Goss-Custard 1970). Frequency and intensity of aggression varies widely between and within shorebird species (Recher and Recher 1969). In this paper we present evidence that an extremely patchy food resource increases the frequency of agonistic encounters in Short-billed Dowitchers (*Limnodromus griseus*), a species which the Rechers describe as rarely aggressive while foraging.

STUDY AREA AND METHODS

Observations were made on 2 tidal sand flats in Kingston and Duxbury bays, near Plymouth, Massachusetts, between 16:00 and 17:45 on 26 July 1976 (Fig. 1). The description of the behavior is based on observations made through spotting scopes at distances of no more than 150 m. To compare the agonistic foragers with controls, we took the number of bird-sec for the group (number of birds being watched multiplied by the time spent watching) and derived an expected ratio of aggressive encounters assuming an equal rate of encounter in each group. The distribution and abundance of food resources available were measured by taking 69 core samples (10 cm diameter, 20 cm deep) of the substrate at 2 m intervals along parallel transects 2 m apart. Each core was broken free of the substrate, washed on a 1.0 mm mesh screen, and sorted by eye in the field. Our previous experience has shown that this procedure removes 90% of the organisms that are greater than 0.25 cm in length (Schneider 1978). Examination of the stomach contents of 3 birds collected on 24 August 1976 showed that more than 70% of the prey items were greater than or equal to 2 mm in length (94, 81, 73%). The 3 stomachs contained 83, 32, and 15 items, ranging in size from smaller than 1 mm to 5 mm.

RESULTS

Description of the behavior.—Dowitchers in this estuary typically forage in cohesive flocks of non-agonistic individuals that move as groups across the flats. We first noticed agonistic behavior in Short-billed Dowitchers in a flock of 125 birds feeding near the SW edge of H-flat. This flock was confined to an area less than 40 m × 10 m. We observed the same behavior at the same site on the 2 subsequent days, occurring in flocks of about 70–80 and 35 birds respectively. The individuals in the flocks were feeding by probing into the sand with their bills using a combination of the probe-multiple-halting (PrMH) and probe-single-halting (PrSH) foraging

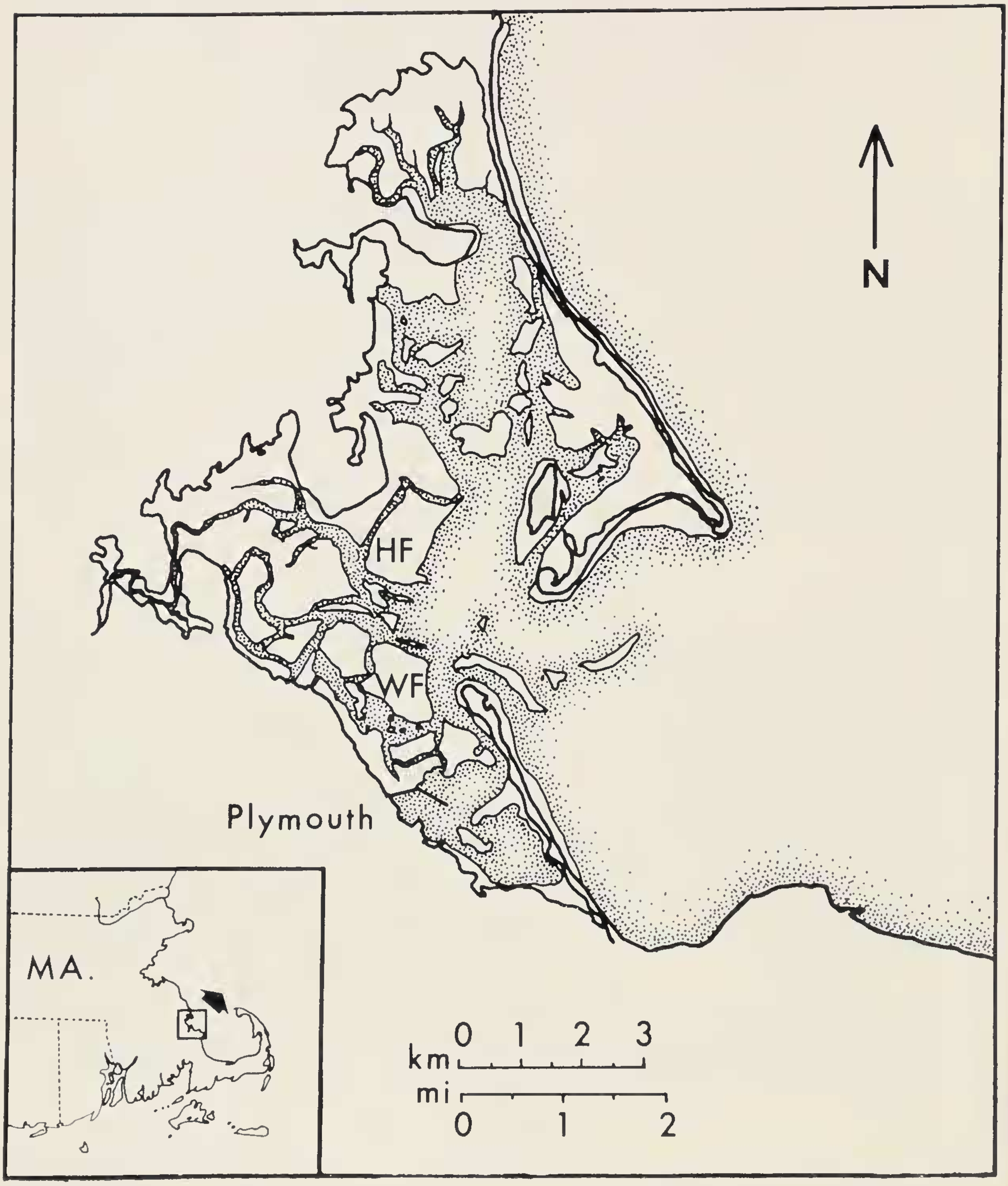

FIG. 1. Locations of H-flat (HF) and White Flat (WF) in Kingston and Duxbury bays where this study was conducted. Inset: location of this estuary on the New England coast.

methods described by Baker and Baker (1973). Individual birds turned frequently, often returning to certain spots to forage rapidly. Aggressive chases were initiated 14 times by successful foragers (seen swallowing after probes) and 15 times by birds intruding on successful foragers. The latter behavior in 10 encounters resulted in a displacement, where an intruder would return to a feeding site after chasing off the successful forager. In 14 other chases the initiator was not determined. In all chases seen, the chaser charged with its body tilted forward so that the tail was above the shoulders but not cocked at the base, wings held against the body, scapular feathers laid flat, neck extended, head low, and bill directed forward and tilted 45° below the horizontal.

Aggressive charges elicited one of 3 responses, all of which prevented direct contact between birds. In 25 of 43 responses to a charge the "chasee" suddenly raised its wings, forming a "V," and jumped up a few decimeters so that only a slight downward stroke of the wings was needed to flutter away a meter or so. In another 17 encounters 1 bird simply ran away, usually less than 1 m. The third response, seen only once, was for a bird to resist displacement by standing its ground. In this circumstance the bird did not remove its bill from the sand but froze as the chaser swerved off from its unsuccessful attack. An agonistic encounter was followed by a repetition of the same behavior, by a reversal when the chasee became the chaser, or by the involvement of a third bird in a second chase.

Other workers in the same bay in 1974 and 1975 observed only 4 instances of aggression involving Short-billed Dowitchers despite approximately 23 h of observation of this species (N. Atkins, pers. comm.; K. Elkins, field notes). None of these instances of aggression resembled the behavior we saw.

Flock dynamics.—We gathered control observations on other flocks of dowitchers during the same tide on H-flat and on another flat in the estuary. One of these flocks, of about 15 birds, was observed foraging immediately following our observations of the agonistic flock on the same sand flat (H-flat), but in an area more normally used by dowitchers. We then observed another flock of about 90 birds foraging on White Flat, a flat similar to H-flat and about 1500 m distant, within 25 min of concluding our observations of the agonistic flock. The area in which these control flocks were feeding had been exposed less than 1 h longer than the area where the agonistic flock foraged. The different flock sizes in our observed groups could be another variable, but in order to make observations close together on the same tidal cycle we had to ignore this possibility.

The number of encounters seen in the agonistic flock and in the control flocks are presented in Table 1. Comparison of the observed rate of encounter with the expected rate showed that there were significantly more encounters (χ^2, $P < 0.005$) in the agonistic flock than in the control flocks (Table 1).

We were impressed by the differences in spacing and movement of individuals in the flock of agonistic birds, relative to control flocks. The

TABLE 1

AGONISTIC ENCOUNTERS WITHIN FLOCKS OF SHORT-BILLED DOWITCHERS[1]

	Mean number of birds watched[2]	Observation period (sec)	Number of encounters[3]	
			Observed	Expected
Flocks foraging on *Limulus* eggs				
H-flat (flock of 70–80)	11.6 (9–17)	670	24	14.27
Same flock	6	370	10	4.07
Total			34	18.34
Flocks not foraging on *Limulus* eggs				
H-flat (flock of 15)	15	120	0	3.30
White Flat (flock of 90)	19.8 (15–23)	395	2	14.36
Total			2	17.66

[1] Observations were made in Kingston-Duxbury Harbor on 26 July 1976.
[2] The range is given in parentheses if the number of birds changed during the observation period.
[3] Expected values were calculated assuming that the number of encounters is proportional to the number of birds watched and the time spent watching them. The observed rate of encounter among foragers on *Limulus* eggs, compared to controls, far exceeds the expected number ($\chi^2 = 29.21 >> \chi^2_{0.005[1]} = 7.88$).

agonistic birds appeared to be concentrated with smaller distances between birds than normally observed, but we did not quantify this. The agonistic birds remained in the same limited area during our observations, while foraging dowitchers at Plymouth often drift slowly across the flats. Finally, the orientation of individuals in the agonistic flock did not coincide, while individuals in control flocks usually moved in the same direction.

Distribution and abundance of food resources.—Sampling carried out on 25 July to determine what food resources were available to the flock of highly agonistic dowitchers showed that potential invertebrate prey items in the area of the flock differed from the surrounding area. Core samples taken from outside the restricted foraging area of this flock contained little besides a few polychaete worms (*Nephthys caeca* and *Scoloplos robustus*) and a few hundred minute gem clams (*Gemma gemma*). All 3 species are far more common in other areas of this and other sand flats in the bay. The 2 samples taken from within the dowitcher foraging area differed only in that 1 of them contained over 50 eggs of the horseshoe crab (*Limulus polyphemus*). We then sampled at 2 m intervals along parallel transects to examine the distribution of the *Limulus* eggs and found 92 eggs in 8 of 14 samples.

We measured egg distribution within the foraging area again on 26 July by sampling at 2 m intervals along parallel transects through the foraging

TABLE 2

DISTRIBUTION AND ABUNDANCE OF IMPORTANT FOOD ITEMS OF SHORT-BILLED DOWITCHERS FORAGING ON H-FLAT AND WHITE FLAT[1]

	Average density ($\bar{x}$) (per 78.5 cm^2 core)	Degree of aggregation[2]
Clymenella torquata (Maldanid polychaete)	2.482	7.438
Tellina agilis (Tellinid pelecypod)	3.827	11.114
Acanthohaustorius millsi (Haustorid amphipod)	7.632	25.383
Trichophoxus epistomus (Phoxocephalid amphipod)	0.897	3.485
Limulus polyphemus eggs (Merostomata: Arthropoda)	0.261	59.832

[1] The importance was judged from stomach contents of dowitchers collected on White Flat and from the high mortality in these species in areas used by dowitchers. Estimates are based on 272 samples from H-flat and White Flat during July, 1976.

[2] Coefficient of dispersion $= s^2/\bar{x}$; $\bar{x} = \Sigma\, x/n$; $s^2 = (x^2 - (\bar{x})^2(n))/(n-1)$; $N = 272$.

area. The 15 cores contained little other than a large number of *Limulus* eggs in 3 adjacent samples. Thus, the occurrence of *Limulus* eggs was not only restricted to a small area of a sand flat, it was also quite patchy within that area. Table 2 indicates how patchy this resource was compared to other prey items of dowitchers feeding on flats in the Kingston-Duxbury estuary.

Limulus eggs were even more localized than indicated by the measure of spatial aggregation used in Table 2. After mating, the female crab deposits 200–300 eggs in a hole of uniform depth gouged into the substrate in a patch that is no wider than 10–20 cm (Shuster 1950). From our observations and sampling efforts, it was apparent that there were several dozen patches of eggs in the area where the agonistic dowitchers were foraging. Spawning sites are evidently quite aggregated since no *Limulus* eggs were collected from over 200 samples made during July of 1976 in the course of a study by DCS of the food resources available to shorebirds in the Kingston-Duxbury estuary.

The occurrence of *Limulus* eggs is also quite restricted in time. Mating and spawning occur monthly, for a few days during spring tides (Hickman 1967). Thus, the resource would only be available to dowitchers once or twice during their summer stay in the estuary.

TABLE 3

CHANGE IN ABUNDANCE OF HORSESHOE CRAB EGGS IN AN AREA OF INTENSE FORAGING BY SHORT-BILLED DOWITCHERS[1]

Date (1976)	Number of eggs collected	Number of samples (with eggs)	Density of eggs per 78.5 cm^2 (variance)	Number of dowitchers
25 July	92	14(8)	6.57(3.96)	125
26 July	19	15(3)	1.22(0.88)	75
27 July	no count			35
6 August	16	20(4)	0.8(0.53)	0

[1] Average egg density was estimated by counting the number of eggs found in the 78.5 cm^2 samples taken at 2 m intervals along 2 parallel transects, each 20 m long, through an area roughly 50 m × 20 m.

Limulus eggs disappeared rapidly from the foraging area on H-flat. Table 3 shows the average density and spatial variation of *Limulus* eggs on 3 succeeding dates, during and after foraging in the area by dowitchers. The average density declined tenfold in 10 days, a significant change (*t*-test, $P < 0.001$). It is possible that the eggs may have been hatching during this period, though no larvae were observed. Our sampling removed 248 eggs, probably a small proportion of the original number. The number of dowitchers feeding at this site decreased as *Limulus* eggs became less abundant (Table 3).

We believe that the flock of unusually agonistic dowitchers was foraging for *Limulus* eggs because (1) these dowitchers confined their activity to a small area where *Limulus* eggs were abundant; (2) other food was far less abundant at this site than in other nearby areas (crustaceans were absent, polychaete worms scarce, and gem clams, the only abundant macroorganism, were an order of magnitude less numerous than elsewhere); (3) the dowitchers were feeding by probing to the full extent of their bills, about 5–6 cm deep, corresponding to the depth of *Limulus* eggs; and (4) dowitchers disappeared from the study site as numbers of *Limulus* eggs declined.

DISCUSSION

We attribute both the change in flock foraging behavior and the increased agonistic behavior of the dowitchers to the patchy distribution of the *Limulus* eggs they were apparently hunting. The restricted dispersion of *Limulus* eggs was probably responsible for the restricted movement of the flock on H-flat. Dowitchers in other areas of the bay foraged in cohesive flocks that moved across the flats. The limited number of food patches generated competition for sites among the birds in the flock because each patch was no larger than an individual dowitcher and there were too few patches to go around. The important differencc for the individuals in the flock was an increased variation in foraging success among birds so that some did very well and some very poorly. A bird standing on a patch would have lower search, capture, and handling times compared to birds not standing on a patch. It is possible that perception of differences in success by dowitchers brought about the increased agonistic behavior we observed.

Recher and Recher (1969) reported a group of Sanderlings (*Calidris alba*) feeding in a similar *Limulus* spawning area (there the eggs were visible on the surface and within the Sanderlings' reach). They concluded that some individuals actually had established feeding territories and excluded other Sanderlings at great expense of time and energy for both groups. It was difficult to ascertain if the dowitchers also had established feeding territories because of (1) the continual mixing of individuals and changes in "roles," and (2) the lack of landmarks on the uniform flat.

The distribution of a food resource appears to influence the amount of agonistic behavior occurring among individuals of a foraging flock. Normally, foraging flocks feed in areas where the prey are not in defendable discrete patches and where 1 bird's success is probably equivalent to its neighbor's. In this case, energy expended in agonistic behavior produces little benefit. However, if food items are distributed in discrete, easily defendable patches, as in the case with *Limulus* cggs, then the cnergetic cost of attempting to acquire or defend a patch may be outweighed by the concentration of a largc number of food items and savings in dccreased search time.

SUMMARY

In this paper wc describe an instanee of unusual, agonistic behavior in a flock of migrant Short-billed Dowitchers (*Limnodromus griseus*). We eompare this behavior to that of other flocks feeding at the same time at other locations in the same estuary and then prcsent evidence suggcsting that this behavior resulted from the patchy distribution of thc probablc foraging resourec of this flock, cggs of the horseshoe erab (*Limulus polyphemus*). We propose that an cxtremcly patchy resourcc has increascd the agonistic behavior within the flock by increasing thc variation in foraging sueeess among individuals.

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LITERATURE CITED

Baker, M. C. and A. E. M. Baker. 1973. Niehe relationships among six species of shorebirds on their wintering and breeding ranges. Eeol. Monogr. 43:193–212.

Goss-Custard, J. D. 1970. Feeding dispersion in some overwintering wading birds. Pp. 3–35 *in* Soeial behavior in birds and mammals (J. H. Crook, ed.). Academie Press, Inc., London.

Hickman, C. P. 1967. Biology of the invertebrates. The C. V. Mosby Co., St. Louis.

Recher, H. F. and J. A. Recher. 1969. Some aspects of the ecology of migrant shorebirds. II. Aggression. Wilson Bull. 81:140–154.

Schneider, D. C. 1978. Selective predation and the structure of marine benthie eommunities. Ph.D. thesis. State Univ. of New York, Stony Brook, N.Y.

Shuster, C. N. 1950. III. Observations on the natural history of the American horseshoe erab, *Limulus polyphemus*. Woods Hole Oceanogr. Inst. Contrib. No. 564:18–23.

MANOMET BIRD OBSERVATORY, MANOMET, MASSACHUSETTS 02345. (PRESENT ADDRESS EPM: DEPT. OF BIOLOGICAL SCIENCES, DARTMOUTH COLLEGE, HANOVER, NEW HAMPSHIRE 03755.) ACCEPTED 1 APR. 1978.